RESEARCH PAPER

Carbon fluxes and their response to environmental variables in a Dahurian larch forest ecosystem in northeast China

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Abstract: The Dahurian larch forest in northeast China is important due to its vastness and location within a transitional zone from boreal to temperate and at the southern distribution edge of the vast Siberian larch forest. The continuous carbon fluxes were measured from May 2004 to April 2005 in the Dahurian larch forest in Northeast China using an eddy covariance method. The results showed that the ecosystem released carbon in the dormant season from mid-October 2004 to April 2005, while it assimilated CO_2 from the atmosphere in the growing season from May to September 2004. The net carbon sequestration reached its peak of 112 $g \cdot m^{-2} \cdot month^{-1}$ in June 2004 (simplified expression of g (carbon)$\cdot m^{-2} \cdot month^{-1}$) and then gradually decreased. Annually, the larch forest was a carbon sink that sequestered carbon of 146 $g \cdot m^{-2} \cdot a^{-1}$ (simplified expression of g (carbon)$\cdot m^{-2} \cdot a^{-1}$) during the measurements. The photosynthetic process of the larch forest ecosystem was largely affected by the vapor pressure deficit (VPD) and temperature. Under humid conditions (VPD < 1.0 kPa), the gross ecosystem production (GEP) increased with increasing temperature. But the net ecosystem production (NEP) showed almost no change with increasing temperature because the increment of GEP was counterbalanced by that of the ecosystem respiration. Under a dry environment (VPD > 1.0 kPa), the GEP decreased with the increasing VPD at a rate of 3.0 $\mu mol \cdot m^{-2} \cdot s^{-1} \cdot kPa^{-1}$ and the ecosystem respiration was also enhanced simultaneously due to the increase of air temperature, which was linearly correlated with the VPD. As a result, the net ecosystem carbon sequestration rapidly decreased with the increasing VPD at a rate of 5.2 $\mu mol \cdot m^{-2} \cdot s^{-1} \cdot kPa^{-1}$. Under humid conditions (VPD < 1.0 kPa), both the GEP and NEP were obviously restricted by the low air temperature but were insensitive to the high temperature because the observed high temperature value comes within the category of the optimum range.

Keywords: carbon balance; eddy covariance method; environmental effect; larch forest; *Larix gmelinii*

Introduction

The dramatic increase in anthropogenic greenhouse gases, especially CO_2, since the industrial revolution has been reported to be

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responsible for the present climate warming. Studies indicated that the carbon of about 5.5 $Gt \cdot a^{-1}$ (simplified expression of Gt (carbon)$\cdot a^{-1}$) is released into the atmosphere from fossil fuels and industrial activity and 1 to 2 $Gt \cdot a^{-1}$ is released from tropical deforestation, of which, about 2 $Gt \cdot a^{-1}$ is removed by the ocean, about 3 $Gt \cdot a^{-1}$ accumulated in the atmosphere. And the remaining 1 to 2 $Gt \cdot a^{-1}$ of "missing carbon" is presumed to be assimilated by temperate and boreal forests (Wofsy et al. 1993; Myneni et al. 2001; IGBP Terrestrial Carbon Working Group, 1998; Tans et al. 1990; Baldocchi et al. 1996; Denning et al. 1995). However, the total amount of the terrestrial ecosystem carbon pool, its spatial distribution pattern, its temporal change, and its response to environmental perturbation are still uncertain. In recent years, with the development of the eddy covariance technique, which offers an alternative way to assess the ecosystem carbon exchange continuously and steadily for a long term, it has become possible to evaluate the carbon balance and its seasonal and annual variation of terrestrial ecosystems more precisely (Baldocchi 2003). Since the 1990s, many studies have been conducted on the net ecosystem carbon exchange between the atmosphere and a variety of terrestrial ecosystems in the temperate and boreal regions (Baldocchi et al. 1988; Kim et al. 1990; Wofsy et al. 1993; Goulden et al. 1997; Baldocchi et al. 1997; Yamamoto et al. 1999; Chen et

al. 1999; Barford et al. 2001; Saigusa et al. 2002; Hirano et al. 2003). The study results have indicated that not all forest ecosystems in the temperate and boreal regions were carbon sinks; some of them were carbon sources on an annual basis or were alternately sources and sinks (Janssens et al. 2001; Falge et al. 2002). Moreover, the net ecosystem carbon exchange varied greatly not only from site to site but also from year to year (Goulden et al. 1997; Yamamoto et al. 1999; Barford et al. 2001; Saigusa et al. 2002).

Temperate and boreal forests demand particular attention in global carbon cycles because they comprise almost 50% of the world forests and are thought to be a major carbon sink (Tans et al. 1990; Baldocchi et al. 1996; Denning et al. 1995). Larch forests are typical in temperate and boreal regions in Eurasia and cover a vast area. In Siberia, Dahurian larch (*Larix gmelinii*) and Siberian larch (*Larix sibirica*) occupy 277.5×10^6 ha^2 (Shvidenko et al. 1994; Gower et al. 1990). Northeast China is the southern distribution edge of Dahurian larch, where larch forests (about 15.6×10^6 ha^2) play a critical role in the natural ecosystem of the region (Jiang et al. 2002). Hence, the carbon budget of the larch forest ecosystem may have a great effect on the global carbon circulation of the terrestrial ecosystem. However, the vast distribution area and large diversity in environmental conditions suggest that there is great variability in the carbon sequestration behavior of larch forest ecosystems. Although some studies have been conducted, the understanding of the carbon cycling process of larch forest ecosystems is still very limited. Hollinger et al. (1998) investigated the carbon balance of a Dahurian larch forest in eastern Siberia with an eddy covariance method for a short period. With the assistance of an ecological model, they estimated that the larch forest was a carbon sink and sequestered carbon of 90 g·m^{-2}·a^{-1}. Hirano et al. (2003) and Wang et al. (2004) investigated the carbon budget of a Japanese larch (*Larix kaempferi*) forest ecosystem in northern Japan using eddy covariance systems (an open-path system for the former and a closed-path system for the latter). Their results indicated that the larch forest ecosystem assimilated carbon of 141 to 293 g·m^{-2}·a^{-1}. Li et al. (2005) recently reported that a Siberian larch forest in a humid and cold montane region of Mongolia sequestered carbon of 85 g·m^{-2}·a^{-1}.

It is well known that many factors may affect the carbon budget of an ecosystem: biotic features, including the leaf area, photosynthetic rate, plant architecture, and type of forest (evergreen or deciduous); and abiotic features, such as radiation, temperature, water supply, soil property, and the length of the growing season. Although the response of carbon fluxes to environmental variables, such as air humidity (or dryness) and temperature, has been reported in some studies (Hollinger et al. 1994; 1998; Chen et al. 1999; Clark et al. 1999; Fan et al. 1995; Wang et al. 2004; Li et al. 2005), quantitative analyses are rare. Therefore, a flux observation program using eddy covariance technology was undertaken in northern Japan (Hirano et al. 2003; Wang et al. 2004), Northeast China (Wang et al. 2005a; 2005b), and Siberia (Kajimoto et al. 2003) to evaluate the current carbon balance of larch forest ecosystems and understand the response of the ecosystem carbon fluxes to environmental variables in

order to accumulate knowledge on the carbon process of larch forest ecosystems, which would allow us to accurately predict the effects of global changes on the whole larch carbon pool and gain insights into climate warming in East Asia. The aim of this study is to characterize the seasonal variation of the carbon fluxes and to evaluate the annual net carbon budget of the Dahurian larch forest ecosystem in Northeast China from May 2004 to April 2005 to quantitatively analyze the response of carbon fluxes to environmental variables.

Materials and methods

Study site

This study was conducted in a Dahurian larch (*Larix gmelinii*) plantation at the Laoshan flux site (LS, 45°20' N, 127°34' E) in Northeast China (Fig. 1). The larch was planted in 1969. The mean height of the canopy trees was about 17 m. The canopy layer was mainly composed of Dahurian larch, paper birch (*Betulla platyphylla*), and Northeast China ash (*Flaxinus mandshurica*). The larch, birch, and ash were composed of 88%, 7.5%, and 4% in basal area and 81.3%, 7.8%, and 6.3% in individual numbers, respectively (Wang et al. 2005a). The shrub layer consisted primarily of *Ulmus propinqua*, *Corylus heterophylla*, *Lonicera ruprechtiana*, *Syringa mandshurica*, *Rubus sachalinensis*, *Sorbaria solbifolia*, *Acanthopanax senticosus*, and *Aralia elata*. The forest floor was covered with abundant herbs, primarily belonging to the *Cyperaceous* and *Liliaceous* families (Shi et al. 2001).

A typical temperate monsoon climate dominates this region. The annual mean precipitation is about 700 mm, and rainfall events occur primarily during the growing season. The annual mean air temperature is 2.8°C. The soil is a typical dark-brown forest soil. The elevation of the site is about 370 m above sea level. The observation tower is located on a south-facing gentle slope of less than 5−6 degrees.

Fig. 1 Location of the Laoshan flux site (LS) in Northeast China

Meteorological and flux measurements

A tower-loaded closed-path eddy covariance system was used to

measure the sensible heat, latent heat, and H_2O and CO_2 fluxes over the larch plantation. The wind velocity and virtual temperature were measured using a three-dimensional ultrasonic anemometer (SAT-550, KAIJO, Japan) at 29 m above ground (about 10 m above the canopy layer). The concentrations of CO_2 and H_2O were measured with a closed-path CO_2/H_2O infrared gas analyzer (IRGA, LI-7000, LICOR, USA) housed in a temperature-controlled box at the top of the tower (20 m high). Air samples were automatically drawn using a diaphragm pump at a flow rate of about 6.5 L·min^{-1} from an air inlet installed at the same height about 40 cm from the anemometer. The inlet was connected to the IRGA via a Dekabon tube that was about 11 m in length and 4 mm in inner diameter. To prevent the condensation of the air sample in the cold and humid conditions, a linear heater was fixed to the entire air sampling tube. The IRGA was operated in a differential mode with CO_2- and H_2O-free N_2 gas flowing through the reference cell. The gain of CO_2 and H_2O in the analyzer was automatically checked once a day by flowing two standard CO_2 gases of 320 ppmv and 420 ppmv. The raw data of the three components of the wind velocity and virtual temperature from the ultrasonic anemometer and the vapor and CO_2 concentrations from IRGA were sampled at 10 Hz, temporally stored in a data logger (CR 23X, CSI, USA), and finally automatically transferred to an online computer every three hours.

The incident and reflected long- and short-wave radiations were measured using a net radiometer (MR-40, EKO, Japan) fixed on the tower at 21 m above ground; the incident and reflected photosynthetic active radiations (PARs) were measured using PAR-02 sensors (PREDE, Japan) at the same height. The PAR transmitted through the canopy was measured in the forest floor at 1 m above ground at 3 locations around the tower. The air temperature (Ta) and relative humidity (RH) were measured at 14 m (within the canopy) and 21 m (above the canopy) with ventilated thermometers and hygrometers (HMP45D, VAISALA, Finland). Precipitation was measured using a rain gauge (YG-52202, YOUNG, USA) installed on the top of the tower at about 22 m above ground. The variation in the air pressure was measured using a barometer (PTB101B, VAISALA, Finland) at 3 m above ground. The soil temperatures (Ts) at depths of 5 cm, 10 cm, 20 cm, and 50 cm were measured using C-PTG-30 (Climatec, Japan). The soil water contents (SWC) at depths of 5 and 20 cm were determined using time-domain reflectometry (TDR) sensors (CS-615, CSI, USA). The variations in the soil heat flux at a depth of 5 cm were detected using soil heat flux sensors (MF-81, EKO, Japan).

Data processing method

CO_2/H_2O fluxes were calculated every half hour from the 10 Hz raw data. To minimize the calculation error, we 1) rejected the noise spikes in the raw data; 2) made a double coordinate rotation to force the vertical wind speed to zero; 3) made a correction for the water vapor concentration; 4) corrected the lag time for the response of the CO_2/H_2O concentrations caused by the long air-sampling tube, and 5) calculated the CO_2/H_2O fluxes as the

covariance of the CO_2/H_2O concentrations and vertical wind speed (Webb et al. 1980; Saigusa et al. 2002; Wang et al. 2004). The carbon storage (Fs) under the canopy was estimated from the temporal difference in the CO_2 concentration measured at the flux plane as previously described (Wang et al. 2004). The net ecosystem CO_2 exchange (NEE) was calculated as the sum of the CO_2 flux (Fc) and Fs, and the net ecosystem production (NEP) is defined as the minus NEE (NEP = –NEE). In this study, the minus sign of NEE indicates the CO_2 uptake by the ecosystem from the atmosphere, and the positive sign indicates the opposite.

Before data analysis, a thorough quality control was carried out. We rejected the flux data associated with the period when the sensors were in trouble, being repaired or calibrated. Spike values caused by electrical problems, rainfall, and other reasons were also removed. Due to the fact that the eddy covariance flux system can not measure the carbon flux properly during the nighttime under the conditions of low atmospheric turbulence (*Goulden* et al. 1996), we examined the response of the nighttime ecosystem respiration (RE) to the friction velocity (u*) in the most vigorous-growth season (from June to August), and a u* threshold of 0.20 m·s^{-1} was determined (Fig. 2). Thus, all nighttime CO_2 flux data with u* values below 0.20 m·s^{-1} were also rejected. As a result, up to 35% of NEE data were lost during the study period.
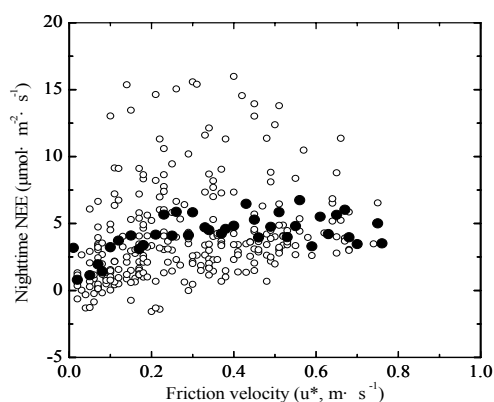

Fig. 2 The response of the nighttime NEE to the corresponding friction velocity (u*) at a temperature range from 10 to 15°C
The open dots indicate the half-hourly data and the solid dots represent the averaged NEE at a u* interval of 0.02 m·s^{-1}.

To evaluate the annual carbon sequestration ability of the larch forest ecosystem, we filled the gaps in the dormant season (both daytime and nighttime) and at nighttime during the growing season using an air temperature-dependent exponential model (RE−Ta), as shown in Eq. (1):

$$R_E = R_0 \times e^{p1 \times Ta} \tag{1}$$

where R_E is the respiration, Ta is the air temperature, and R_0 and p_1 are empirical parameters. This equation will be discussed in the following section.

Those gaps in the daytime of the growing season were filled following a PAR-dependent saturation model (NEE−PAR) as shown in Eq. (2):

$$N_{EE} = -b_1 \times P_{AR}/(P_{AR}+b_1/b_2) + b_0 \qquad (2)$$

where b is generally considered as the potential maximum photosynthetic capacity, b_2 is the initial light-use efficiency, and b_0 is a respiration parameter. The empirical parameters obtained according to Eq. (2) in different months of the growing season are shown in Table 1.

Table 1. Parameters for the best-fitted curves using Eq. (2) to describe the relationships between the NEE and incident PAR at the LS site in different growing seasons from May 2004 to April 2005

Growing period	b_1 ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	b_2 ($mol \cdot mol^{-1}$)	b_0 ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	r^2
May 1 to 10, 2004	13.67	0.0129	2.23	0.6912
May 10 to 31, 2004	26.28	0.0509	3.37	0.6945
June 2004	26.86	0.0404	3.74	0.649
July 2004	35.06	0.0478	5.22	0.77
Aug 2004	27.53	0.0365	3.31	0.6124
Sep 2004	28.38	0.0318	3.25	0.6421
Oct 1 to 15, 2004	22.74	0.0114	2.89	0.4873

Notes: The NEE gaps in the daytime of the growing season were filled based on these relationships.

To precisely characterize the seasonal variation of the photosynthetic rate, we parameterized the relationship between the gross ecosystem production (GEP) and absorbed photosynthetic active radiation (APAR) following the standard Michaelis-Menten model (Hollinger et al. 1994; 1998):

$$G_{EP} = \alpha \times A_{PAR}/(A_{PAR}+\alpha/\beta) \qquad (3)$$

where α is the potential maximum photosynthetic capacity and β is the initial light-use efficiency.

The A_{PAR} was calculated from the incident P_{AR} after accounting for the reflected and transmitted portions of the canopy. The G_{EP} was calculated from the difference between the daytime ecosystem respiration (R_E) and NEE ($G_{EP}=R_E-N_{EE}$), while the daytime RE in the growing season was estimated using the RE−Ta model (Eq. (1)) following previous studies (Janssens et al. 2001; Saigusa et al. 2002; Wang et al. 2004). The daytime respiration is likely to differ from the nighttime respiration because of light-induced inhibition on leaf respiration (Brooks et al. 1985). Therefore, this extrapolation of nighttime respiration may cause an overestimation of the daytime respiration. This overestimation depends on the contribution of leaf respiration to the total respiration and on the degree of light-induced inhibition. Thus, the degree of the overestimation could not be properly evaluated at present (Wang et al. 2004).

To understand the variation pattern of the leaf area index (LAI) of the larch canopy, we periodically measured the plant area index (PAI) using a plant canopy analyzer (LAI-2000, LICOR, USA) weekly in May and monthly in the other season. Using Beer's law (Eq. (4)), the extinction coefficient, k = 0.83, was calculated from the PAI and the corresponding extinction of the PAR, which was continuously measured below and above the canopy.

$$P_{AI} = -1/k \times LN (T_{rPAR}/P_{AR}) \qquad (4)$$

where, k is the extinction coefficient, T_{rPAR} the PAR transmitted through the canopy, and PAR is the incident P_{AR} (the daytime mean value was used for this study). The P_{AI} measured in the leafless season was considered to be the woody area index (W_{AI}=1.14). Thus, the L_{AI} was obtained from the P_{AI} after accounting for the W_{AI} (Hirano et al. 2003; Wang et al. 2004).

Results and discussion

Seasonal variation of the CO$_2$ flux and environmental variables

The LS locates in Northeast China, where a monsoon climate dominates. Fig. 3 shows the seasonal courses of the daily mean environmental variables and NEE at the LS during the study year (from May 1, 2004, to April 30, 2005). The daily mean APAR, Ta, Ts, VPD, SWC, and LAI are obviously higher during the growing season (from May to the first half of October 2004) than that in winter. Correspondingly, the NEE was negative during the growing season and turned positive during the dormant season.

The daily mean APAR was generally lower than 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the dormant season and much higher in the growing season. The monthly mean APAR was 488 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in June, much higher than that in any other months. The coldest season was January and February with monthly mean Ta as low as −16.6°C and the hottest season were June and July with mean Ta of 21.0°C and 20.7°C, respectively. The highest daily mean Ta was 26.3°C observed on June 16 (DOY 168), and the lowest daily mean Ta was −27.2°C observed on December 22 (DOY 357), 2004. However, the soil temperature (Ts) at a 5-cm depth was not low even in winter due to the heat preservation effect of a 30- to 50-cm snow cover. The monthly mean Ts was below zero during the period from January to March with a minimum daily mean Ts of −1.1°C. The Ts began to rise in spring soon after the snow melting with increasing radiation and reached the highest monthly Ts value of 17.4°C in August.

In the growing season of 2004 (from May to September), the maximum daily mean VPD was 2.2 kPa on June 13 (DOY 165), and the extreme half-hour value even reached 3.5 kPa. While inspecting the monthly values, it is found that the VPD in June averaged 1.33 kPa, which was much higher than that in the other growing months (0.81, 0.59, 0.69, and 0.68 kPa in May, July, August, and September, respectively). The extremely high VPD in June was mainly caused by the lack of rainfall (20.2 mm·month^{-1}).

The soil water content (SWC) was generally low during the cold season. The SWC increased with snow melting and reached a peak of about 0.55 m$^3 \cdot$m^{-3} at the beginning of May after a continuous rainfall event. The SWC then gradually decreased with the soil water consumption via evapotranspiration and rapidly recovered again soon after another rainfall event.

The LAI increased from late April and reached a maximum of about 2.5 m$^2 \cdot$m^{-2} in late May and the beginning of June. About 3 months later, the LAI of the larch forest began to decrease at the beginning of September, and the foliage completely withered and

fell in mid-October.

Obviously, the larch forest ecosystem was a carbon source in the dormant season from late October 2004 to April 2005 (Fig. 3). It generally released carbon of less than 1 $g \cdot m^{-2} \cdot d^{-1}$ (simplified expression of g (carbon)$\cdot m^{-2} \cdot d^{-1}$) during the cold months from December 2004 to February 2005, but more was released in the other dormant months with a relatively warmer climate. For example, the ecosystem released as much as 2.4 $g \cdot m^{-2} \cdot d^{-1}$ in October. Despite the soil and air temperatures below 0°C for the periods from January to February 2005, the ecosystem still released carbon to the atmosphere, which was attributed partially to the activity of soil microbes with a high tolerance to severe conditions (Zimov et al. 1993; Fang et al. 1999). With the increase of PAR and air and soil temperature, the trees began to leaf out in late April, as indicated by the increasing LAI, and the larch forest ecosystem then rapidly switched from a carbon source to a sink in May. The ecosystem reached the maximum carbon uptake of 3.7 $g \cdot m^{-2} \cdot d^{-1}$ in June. After then, it gradually decreased and completely switched to zero in early October. This seasonal variation pattern of NEE at LS is very similar to that of a Japanese larch forest ecosystem in northern Japan, where the carbon sequestration also peaked in June (Wang et al. 2004).

growing season, however, large variations in the NEE were observed. Generally, the ecosystem changed from a nighttime carbon source to a daytime carbon sink. The maximum values were observed around noon for the APAR, after noon for the temperature and VPD, and before noon for the NEE and GEP, when the temperature (Ta and Ts), PAR, and VPD were not very high. This implies that the high temperature and VPD probably affected the carbon assimilation of the ecosystem.

The diurnal maximum NEP and GEP of the ecosystem were 16.8 and 24.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in July, 15.9 and 24.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in June, and 14.7 and 22.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in August, obviously higher than the values of 11.9 and 17.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in May and 13.4 and 18.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in September, respectively. In May and October, the low carbon uptake rate and GEP were mainly ascribed to the low LAI (for May and October) and leaf senescence (for October). The LAI was only about 1.4 $m^2 \cdot m^{-2}$ in May and 1.8 $m^2 \cdot m^{-2}$ in October, but it was 2.3 to 2.5 $m^2 \cdot m^{-2}$ in the summer from June to August. On the other hand, the ecosystem respiration in mid-summer was also much higher than that in other months due to the warm climate. The diurnal maximum RE values were 9.6, 8.7, and 8.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for June, July, and August, respectively, but decreased to 6.2 and 5.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for September and May, respectively.
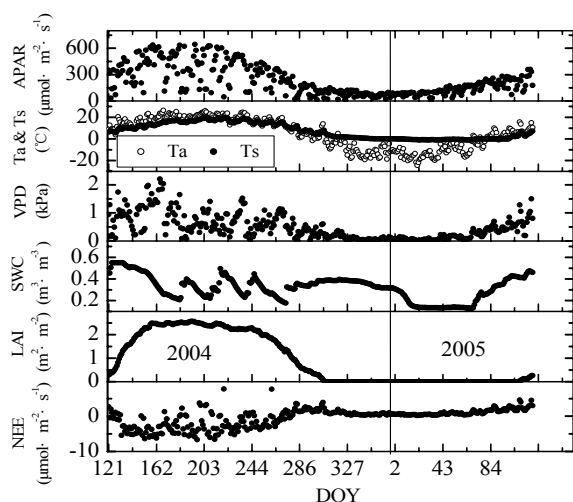

Fig. 3 Seasonal variation of the daily mean absorbed photosynthetically active radiation (APAR), temperature in air (Ta) and soil (Ts), vapor pressure deficit (VPD), soil water content (SWC), canopy leaf area index (LAI), and net ecosystem exchange (NEE) of the larch forest in Northeast China from May 1 (DOY 121), 2004, to April 30 (DOY 120), 2005

Diurnal course of the CO₂ flux and environmental variables

To describe the feature of the diurnal pattern of carbon fluxes, monthly ensemble-averaged half-hourly carbon fluxes, including NEE, RE, and GEP, and the corresponding PAR, Ta, Ts, and VPD from April (in 2005), May (in 2004) to October (in 2004), are shown in Fig. 4. In dormant months (April and October), although the ecosystem obviously absorbed carbon in early October, it mainly acted as a carbon source in most days of October and there were few changes in the NEE within a day. In the
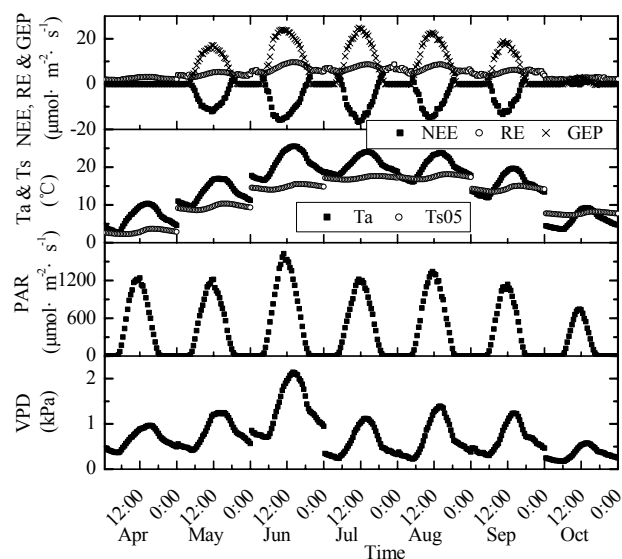

Fig. 4 Diurnal courses of monthly ensemble-averaged absorbed photosynthetic active radiation (APAR), air temperature (Ta), soil temperature (Ts), vapor pressure deficit (VPD), and net ecosystem exchange (NEE) of the larch forest at the LS from April (in 2005), May (in 2004) to October (in 2004)

The day length varies with the season. Correspondingly, the net carbon uptake duration of a day (NCUD, defined as the hours with NEP > 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ within a day) in the growing season also varied. The mean daily NCUD during the growing season was 12.5 $h \cdot d^{-1}$ in May and peaked to 13.5 $h \ d^{-1}$ in June but was reduced to 11.5 $h \cdot d^{-1}$ in July and August and 10 $h \cdot d^{-1}$ in September.

Response of the ecosystem respiration to the temperature

The ecosystem respiration has been reported to be very sensitive to temperature changes in many ecosystems, and the relationship between ecosystem respiration and temperature has usually been described using an exponential model (Baldocchi et al. 1997; Hollinger et al. 1994; Chen et al. 1999). Fig. 5 shows that the ecosystem respiration increased with the air temperature at LS. The Q_{10} was estimated to be 1.7; this value is quite lower than that of a Dahurian larch forest in east Siberia (2.3) (Hollinger et al. 1998), of a Japanese larch forest in northern Japan (3.0) (Wang et al. 2004), of a boreal jack pine forest (2.6) (Baldocchi and Vogel, 1996), and of a temperate deciduous broadleaved forest in central Japan (2.6), (Saigusa et al. 2002). The exact reason for the quite low Q_{10} at LS is under investigation.

Considering the possible influence of the soil water content (SWC), the relation between the RE and Ta under different SWC levels were examined during the growing season from June to August 2004. However, we could not find any obvious effect of the SWC (the figure was omitted).
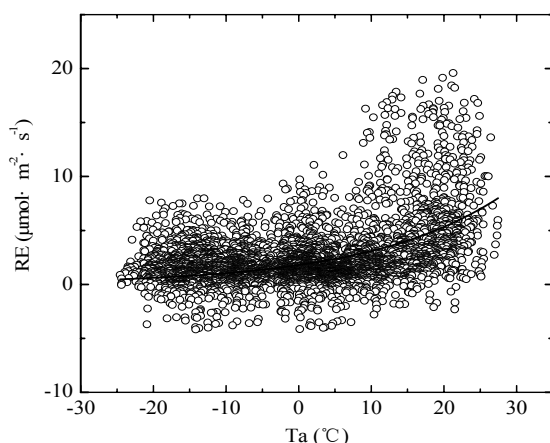

Fig. 5 Larch forest ecosystem respiration (RE) as a function of the air temperature (Ta) under the condition of strong turbulence (u*>0.20 m·s⁻¹) at the LS.

The best-fitted exponential curve is $R_E = 1.7911 \times e^{0.0545 \times Ta}$. The NEE gaps in the dormant season and in the nighttime of the growing season were filled based on this relationship.

Response of GEP to APAR

Two flux components, ecosystem respiration (RE) and photosynthetic ability (or GEP), are necessary to determine whether an ecosystem will act as a net carbon sink or source. Although many environmental factors may affect the photosynthesis of an ecosystem, light is generally the key factor. To elucidate the response of the photosynthesis of the larch forest ecosystem to light, we correlated the GEP with the APAR using Eq. (3) in different growing stages, and the parameters for those best-fitted curves are given in Table 2. The initial light-use efficiency (β) was the highest (0.067 mol·mol⁻¹ (simplified expression of mol (CO_2) ·mol⁻¹(photons)) in June, followed by 0.060 mol·mol⁻¹ in July,

and the lowest in October (0.011 mol·mol⁻¹) and the first ten days in May (0.027 mol·mol⁻¹). The potential maximum photosynthetic capacity (α) of the larch forest during this study period was the highest (40.63 μmol m⁻² s⁻¹) in July, followed by 34.78 μmol·m⁻²·s⁻¹ in August and 33.23 μmol·m⁻²·s⁻¹ in September, and the lowest in the first ten days in May. However, α value was only 31.89 μmol·m⁻²·s⁻¹ in June 2004 and even lower than that in September. On the other hand, for June 2002, it was estimated to be 41.92, 46.82, and 56.54 μmol·m⁻²·s⁻¹ when the VPD > 2.0 kPa, 1.0 < VPD <2.0 kPa, and VPD < 1.0 kPa, respectively (Wang et al. 2005b). Considering the extremely high air temperature and VPD (Figs. 3 and 4), it seems that the photosynthetic rate of the larch forest ecosystem in June 2004 was abnormal and might be strongly affected by these environmental variables.

Table 2. Empirical parameters for the relationships between the GEP and APAR, which were best-fitted using a Michaelis-Menten model (Eq. 3) in different growing seasons at the LS site

Growing period	α (μmol·m⁻²·s⁻¹)	β (mol·mol⁻¹)	r^2
May 1 to 10, 2004	18.01	0.027	0.7045
May 10 to 31, 2004	30.89	0.057	0.7635
June 2004	31.89	0.067	0.7425
July 2004	40.63	0.060	0.817
Aug 2004	34.78	0.055	0.7276
Sep 2004	33.23	0.044	0.7115
Oct 1 to 15, 2004	592.77	0.011	0.5607

Notes: In this table, α is the maximum photosynthesis ability (μmol·m⁻²·s⁻¹), and β is the initial light-use efficiency (mol·mol⁻¹).

Response of the NEE and GEP to the VPD and air temperature

In addition to radiation, the VPD and air temperature are generally considered to be the most important environmental factors affecting the ecosystem photosynthesis process. However, it is not easy to separate the total environmental effects into individual factors due to the interactions among these factors (Chen et al. 1999). Two methods are usually used to evaluate the effects of the VPD and air temperature on the ecosystem photosynthesis. One is to remove the effect of light from the observed CO_2 fluxes (GEP or NEE) according to the light-dependent photosynthesis curves and then to analyze the relationships between the residue flux data and VPD or air temperature (Hollinger et al. 1994; 1998). However, the light-dependent photosynthesis curves of an ecosystem were generally determined from the measured carbon fluxes and the corresponding light, while the carbon fluxes were determined by all environmental variables rather than by light alone. Therefore, some uncertainties and biases inevitably exist.

Another method is to correlate the carbon flux data obtained under light-saturated conditions with the corresponding environmental factors (Fan et al. 1995; Clark et al. 1999). Theoretically, this method is more reasonable because the importance of an environmental factor in an ecological process is alterable with environment changes (Li et al. 2000). Under light-saturated con-

ditions, environmental variables other than radiation will dominate the photosynthetic process. In this study, the latter method was applied.

Fig. 6 shows the responses of the NEE and GEP of the larch forest ecosystem to the VPD under saturated light conditions (PAR > 700 μmol·m^{-2}·s^{-1}) in the vigorous-growth season (June to August 2004). Clearly, neither the NEE nor the GEP was simply linearly correlated with the VPD. The GEP increased with the increasing VPD at a rate of 3.7 μmol·m^{-2}·s^{-1}·kPa^{-1}, but the NEE maintained a nearly constant value of about −18.3 μmol·m^{-2}·s^{-1} when the VPD was lower than 1.0 kPa. On the other hand, when the VPD increased more than 1.0 kPa, both the GEP and the NEP decreased linearly. The GEP decreased at a rate of 3.0 μmol·m^{-2}·s^{-1}·kPa^{-1}, while the NEP decreased more rapidly at a rate of 5.2 μmol·m^{-2}·s^{-1}·kPa^{-1} with the increasing VPD.

The different responses of the GEP and NEP to the VPD under low and high VPD levels indicated that some other environmental factors were affecting the carbon process. Considering the linear relationship between the Ta and the VPD (Fig. 6), we inferred that the temperature might be the factor affecting the NEE and GEP under suitable VPD conditions (VPD < 1.0 kPa). Under low-VPD and light-saturated conditions, the variation in both humidity and light environments should have a lesser or no effect on the GEP; therefore, it is reasonable to believe that the rising temperature accompanying the VPD should be responsible for the increment in the GEP.
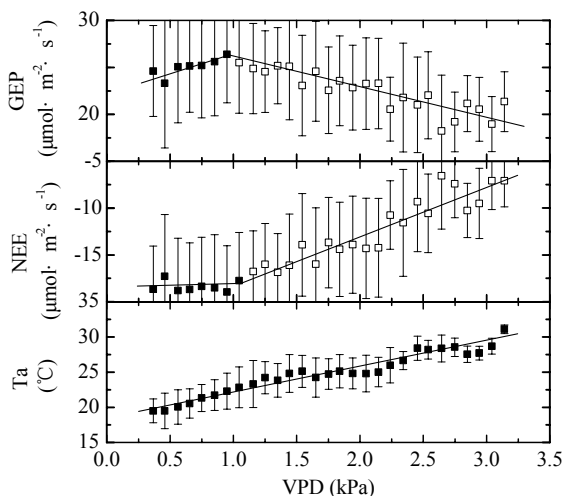
and the respiration with the increased temperature were quite similar in quantity and offset each other, thus resulting in the relative constant NEE value with the VPD variation. However, when the VPD exceeded 1.0 kPa, the dryness controlled the photosynthesis, and the GEP declined with the increasing VPD at a relatively slow rate. By contrast, due to the increased ecosystem respiration with the increased temperature, the NEP decreased more rapidly with the increasing VPD.

To further confirm the influence of the temperature on the ecosystem CO_2 fluxes, the responses of GEP and NEE to the air temperature were plotted and best-fitted under the conditions of beneficial humidity (VPD < 1.0 kPa) and saturated radiation (PAR > 700 μmo·m^{-2}·s^{-1}), as shown in Fig. 7. Obviously, the GEP was improved with the increasing temperature under humid conditions, and the low temperature greatly restricted the photosynthetic ability of the larch forest ecosystem. The maximum GEP was estimated to be 28.18 μmol·m^{-2}·s^{-1} when the air temperature reached 30.5°C. Here, we define the environmental condition under which the GEP reaches 80% or more of the maximum value as the optimum environment. The optimum temperature for the photosynthesis of the larch forest ecosystem was estimated to be from 18 to 42.5°C. But the reliability for the upper limit of the optimum temperature is uncertain due to the lack of observation data.
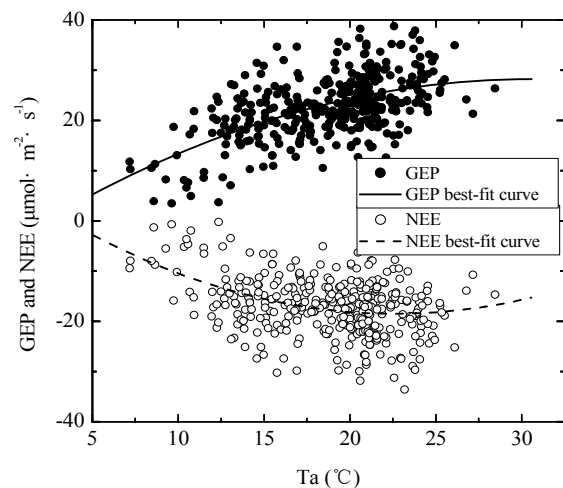

Fig. 7 The response of GEP and NEE to Ta under the conditions of saturated radiation (P_{AR} > 700 μmol·m^{-2}·s^{-1}) and humid air (V_{PD}<1.0 kPa) at the LS (data obtained during the vigorous-growth period from June to August 2004 were used)
The filled circle and solid curve for G_{EP}, while the open circle and dash curve for N_{EE}. The best-fitted curves: G_{EP}=−0.0354×Ta^2 +2.1565×Ta−4.6633 (r^2=0.3232, P<0.0001), and N_{EE}=0.0506×Ta^2−2.2896×Ta+7.3910 (r^2=0.1464, P<0.0001).

On the other hand, the response of the NEE, the residue between the GEP and the RE, to the temperature was somewhat different from that of the GEP. The minimum NEE was estimated to be −18.51 μmol·m^{-2}·s^{-1} when the air temperature was 22.6°C based on the NEE-Ta relationship. Therefore, a moderate air temperature seemed more beneficial for the ecosystem carbon

Fig. 6 Variation of the mean Ta, NEE, and GEP with a vapor pressure deficit (VPD) under light-saturated conditions (PAR>700 μmol·m^{-2}·s^{-1}) at LS in summer (from June to August) of 2004
The dotted data were block-averaged at a VPD range of 0.1 kPa, and the dark lines were best-fitted curves. The best-fitted results were: G_{EP} = 3.743×V_{PD} + 22.592 (r^2 = 0.6807); N_{EE} = −0.083×V_{PD} − 18.313 (r^2 = 0.162) when V_{PD} <= 1.0 kPa, G_{EP} = −2.954×V_{PD} + 28.639 (r^2 = 0.7937) and N_{EE} = 5.239×V_{PD} − 23.433 (r^2 = 0.8933) when V_{PD}>= 1.0 kPa, and Ta = 3.478×V_{PD} + 18.711 (r^2 = 0.9368) for all V_{PD} data.

However, the increased temperature also enhanced the ecosystem respiration. It seems that the portion of the increased GEP

uptake. Similar to that of the GEP, the optimum temperature for the ecosystem carbon uptake was estimated to be from 14 to 31.5°C. The low temperature obviously reduced the GEP and the NEP. On the other hand, the insensitiveness of the NEP and GEP to high temperature could be ascribed to the fact that the increment in the ecosystem respiration and that in GEP caused by enhanced temperature offset each other.

The effects of the VPD (dryness stress) and temperature (heat stress) on the CO_2 fluxes (GEP or NEE) have received a considerable amount of attention. A quantitative evaluation on the effect of the VPD, temperature and other environmental factors on the ecosystem carbon fluxes is very important for understanding the ecosystem carbon process and creating a precise ecological model, but this kind of study is infrequent. Some reports have indicated that the relationships between the CO_2 fluxes and the VPD (and/or temperature) were simply linear (Hollinger et al. 1994; Clark et al. 1999). Fan et al. (1995) noticed the existence of a VPD threshold (about 0.6 kPa) to the photosynthesis of a boreal dark-spruce forest, but they indicated that the light-saturated photosynthesis of the boreal forest during periods of low evaporative demand (VPD<0.6 kPa) was unrelated to the air temperature. This is clearly not the case for the larch forest ecosystem. The increase in the temperature obviously improved the photosynthesis of the larch forest. The threshold of the VPD of the Dahurian larch forest ecosystem is obviously lower in Northeast China (1.0 kPa) than in eastern Siberia (about 2.5 kPa) (Hollinger et al. 1998). The same tree species exhibited greatly different abilities to endure the dryness due to their long-term adaptation to the local environment.

Monthly and annual carbon sequestration

Monthly statistics showed that the ecosystem released 15, 28, 43, and 48 g·m^{-2}·month^{-1} from January to April 2005 (Table 3). However, the ecosystem soon switched to a large carbon sink in May with the foliation. The GEP, RE, and NEE of the larch forest ecosystem were 331, 219, and –112 g·m^{-2}·month^{-1} in June, 306, 228, and −79 g·m^{-2}·month^{-1} in July, and 279, 212, and −67 g·m^{-2}·month^{-1} in August, respectively. Although the air temperature was the highest in June, the soil temperature was lower than those in July and August. Thus, the amount of the ecosystem respiration in June was similar to that in August but lower than that in July. Furthermore, the abundance of incident radiation and the high initial light-use efficiency obviously improved the photosynthesis of the larch forest ecosystem and resulted in a higher GEP in June than in July and August. As a result, the NEP in June was much higher than that in July and August.

However, the net carbon uptake value in June was quite low in 2004 (112 g·m^{-2}·month^{-1}) when compared with that in 2002 (184 g·m^{-2}·month^{-1}), (Wang et al. 2003). Our previous analysis indicated that both the GEP and NEE of the larch forest ecosystem were sensitive to the VPD and temperature. Considering the weather condition in June 2004 (monthly VPD=1.33 kPa, Ta=21.0°C), it is reasonable to believe that the high VPD and air temperature restricted the carbon uptake of the ecosystem.

In May 2004, the larch leaf was not fully developed, especially

in the first ten days, and the monthly GEP was only 216 g·m^{-2}·month^{-1}. Clearly, the lack of green leaves greatly limited the ecosystem photosynthesis. However, the monthly NEP in May produced the second highest value of 81 g·m^{-2}·month^{-1}, even higher than that in July and August, due to lower ecosystem respiration. In October, the carbon sequestration ability was rapidly reduced because of the leaf senescence and leaf fall, and the ecosystem completely turned to a carbon source in the mid-October.

Table 3. Monthly and annually accumulated NEE, RE, and GEP of the Dahurian larch forest ecosystem at the LS from May 2004 to April 2005 (g·m^{-2}·month^{-1})

Month	NEE	RE	GEP
Jan	15	15	0
Feb	28	28	0
Mar	43	43	0
Apr	48	48	0
May	-81	135	216
Jun	-112	219	331
Jul	-79	228	306
Aug	-67	212	279
Sep	-37	156	193
Oct	49	75	26
Nov	32	32	0
Dec	16	16	0

Annually, the larch forest ecosystem was a carbon sink and sequestered carbon of 146 g·m^{-2}·a^{-1} in the period from May 2004 to April 2005. This value is much higher than 90 g·m^{-2}·a^{-1} for a Dahurian larch forest in Siberia (Hollinger et al. 1998) and 85 g·m^{-2}·a^{-1} for a Siberian larch (Larix sibirica) forest in east Mongolia (Li et al. 2005) but is quite similar to the value of 141 g·m^{-2}·a^{-1} observed at a Japanese larch forest ecosystem in northern Japan (Wang et al. 2004). Considering the large inter-annual variation in the NEE (Goulden et al. 1997; Yamamoto et al. 1999; Barford et al. 2001) and the extremely dry environment in June 2004, it is difficult to reach a definite conclusion on the basis of the results of one year alone, and long-term flux monitoring of the ecosystem is obviously needed. Moreover, we are also conscious of the uncertainty of our annual carbon budget results that may be affected by the slightly complex geographical conditions of the observation site. Although we used a large friction velocity(u*) threshold (0.20 m·s^{-1}) to screen flux data, possible advection may also have occurred, especially on stable and weak-wind nights (Lee et al. 1998; Baldocchi 2003). Therefore, further effort is needed to evaluate the possible advection and its possible effect to the annual carbon budget at the site. This is also a challenge for many other forest flux sites, as most of them were built on complicated topographical locations.

Conclusions

The net ecosystem exchange of the larch forest ecosystem at the LS varied seasonally. The larch forest ecosystem acted as a carbon source in the dormant season from October 2004 to April

2005 but converted to a carbon sink during the growing season. Annually, it was a carbon sink during the year from May 2004 to April 2005 and assimilated carbon of 146 g·m^{-2}·a^{-1}. June was the most important month for carbon assimilation of the ecosystem, when the carbon uptake shared 77% of the annual accumulated amount. This could be ascribed to the high light-use efficiency, sufficient radiation, and long NCUD of a day (13.5 h·d^{-1}). However, the extremely high VPD in June tended to lower the GEP. Environmental variables had a significant influence in the carbon fluxes of the larch forest ecosystem. The ecosystem respiration was mainly determined by temperature following an exponential pattern. The GEP varied with the APAR following a saturation model. The responses of the GEP and NEE to the VPD were found to be different in different VPD thresholds. Under saturated light and humid conditions (VPD < 1.0 kPa), the GEP increased with the increasing VPD because the enhanced temperature, which was linearly correlated with the VPD, improved the photosynthetic ability of the ecosystem, while the NEE was only slightly affected by the VPD variation because the increment in the GEP and RE with the increasing temperature offset each other. On the other hand, when the VPD exceeded 1.0 kPa, the restriction from dryness controlled the photosynthesis, and the GEP declined with the increasing VPD at a rate of 3.0 μmol·m^{-2}·s^{-1}·kPa^{-1}. Correspondingly, the NEP decreased more rapidly with the increasing VPD at a rate of 5.2 μmol·m^{-2}·s^{-1}·kPa^{-1} due not only to the reduced GEP but also to the enhanced ecosystem respiration with the increasing temperature. The beneficial condition for the larch forest ecosystem photosynthesis and net carbon uptake was VPD < 1.0 kPa. The optimum air temperature for the net carbon uptake of the Dahurian larch forest ecosystem was estimated from 14 to 31.5°C at LS. These quantitative parameters of the VPD and air temperature for the larch forest ecosystem GEP and NEE are obviously very important for understanding the characteristics and mechanisms of the larch forest ecosystem carbon cycling process and for parameterzing ecological models to simulate and predict carbon fluxes so as to more precisely extrapolate regional observation results.

Acknowledgement

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